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ROOT SUCKERING IN YOUNG ASPEN, GIRDLED, DEFOLIATED, AND DECAPITATED AT VARIOUS SEASONS

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Abstract: Effect of various treatments on suckering by young aspen (Populus tremuloides Michx.) growing in pots was determined at different seasons. Girdling or decapitation during shoot elongation resulted in sucker formation a few weeks later. Defoliation or removal of shoot tips during shoot growth did not induce suckering. All treatments stimulated sucker initiation in dormant plants, but shoot growth was suppressed until the following spring even though temperatures were favorable. Decapitated plants produced more than twice as many suckers, of superior growth, than girdled plants. Fall application of indole-3-acetic acid (IAA) to the stumps of dormant plants dramatically inhibited stump sprouting but not root suckering.

Additional keywords: Populus tremuloides, adventitious shoots, stem sprouts, indole-3-acetic acid.

There is substantial evidence that the development of suckers (adventitious shoots) on roots of aspen (Populus tremuloides Michx.) is suppressed by auxin translocated from aerial parts, a phenomenon known as apical dominance (Farmer 1962; Eliasson 1971a, 1971b, 1972; Schier 1973c, 1975). Auxin is synthesized in swelling buds, in growing shoots, and in leaves (Eliasson 1971a), and is transported to the roots in the assimilate stream via the phloem (Eliasson 1972). Suckers in aspen roots principally arise from preexisting or currently initiated meristems that frequently do not develop beyond the primordial stage (Schier 1973b). Suckers are probably initiated by cytokinins, hormones that are synthesized in root tips (Peterson 1975; Skene 1975; Williams 1972). High cytokinin-auxin ratios favor shoot initiation; low ratios inhibit it (Winton 1968; Wolter 1968).

It has been shown that when the tops of aspen are removed or girdled, root suckers are induced in response to a decrease in auxin concentration (Farmer 1962; Eliasson 1971b). However, most treatments were carried out when shoot elongation was occurring. We do not know if the season of treatment affects suckering. Therefore, a series of experiments were conducted on young aspen to determine the effects of girdling, decapitation, and defoliation at various seasons on sucker initiation and growth.

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A single clone of aspen was used in the following experiments. Plants were propagated in a greenhouse by culturing suckers from root segments, rooting sucker cuttings, and planting rooted cuttings in a sand:peat (1:1) medium in 1 gal (3.8 ℓ) pots. Periodic watering and fertilization maintained the plants in a healthy condition. Unless otherwise mentioned, the experiments were performed in the greenhouse where the diurnal air temperature varied from 15° to 25°C. Plants were overwintered in pits in a lathhouse. Pots were buried in wood shavings to prevent abnormal freezing or cracking of the pots. Two-year-old plants were used in all experiments.

In each experiment differences in sucker production caused by treatment were tested by analysis of variance. Significance of differences between ranked means was determined by Kuels' method (Snedecor 1956). A square root transformation was applied to numbers of suckers or sprouts prior to analysis.

Experiment I

Method.--The effect of girdling and decapitation on sucker production by aspen was determined by treating plants (mean ht, 137.7 cm; mean dia at 3 cm, 13.2 mm) on July 12, 1973. Shoot elongation was still in progress. There were 18 plants per treatment, including controls. Stems of decapitated plants were severed just above the root collar. Exposed tissue was covered with petroleum jelly. Plants were girdled by peeling off 1 cm of bark just above the root collar. The bared xylem surface was scraped with a razor blade to remove residual cambial tissue. The wound was protected with petroleum jelly and the girdled area was covered with aluminum foil. After 42 days, the soil was washed from the roots of each plant and the number of suckers counted.

Results.--The mean number of suckers produced by treated plants was as follows: control, 0; girdled, 19.8; decapitated, 49.7. Differences among treatments were significant. Roots of the girdled plants looked unhealthy. Most of the fine roots had died and decay was present in the larger roots. There was a proliferation of callus tissue in the stems above the girdles, and in a few cases adventitious roots had been initiated, indicating the accumulation of auxin. Mean shoot growth was 53.8 cm for control plants and 10.4 cm for girdled ones.

Experiment 2

Methods.--Effects of removing foliage and shoot apices on sucker production by aspen was determined by treating plants (mean ht, 172.0 cm; mean dia at 3 cm, 13.4 mm) on June 17, 1974. Shoot elongation was occurring at this time. The treatments (7 plants/treatment) were as follows:

1. Control.

2. Single defoliation - removed all leaves.

3. Two defoliations - three weeks after the initial defoliation, when the second set of leaves had flushed out, the new leaves were also removed.

4. Apical removal - excised 5 cm from the tops of all terminal and lateral shoots.

5. Apical removal and a single defoliation.

On August 19, 9 weeks after the initial treatment, the soil was washed from the root system of each plant and the roots examined for suckers.

Results.--Neither root suckers nor stem sprouts from suppressed buds were found on any of the treated plants. Roots were closely examined to determine if shoot primordia were present. None could be found; however, it is possible they were too small to be detected.

All plants from which parts were removed showed a new flush of growth from dormant buds. Even plants defoliated twice put out a third set of leaves, although they were smaller than normal and greatly reduced in numbers compared to the controls.

Experiment 3

Methods.--The effect of girdling, defoliation, and decapitation on suckering by aspen was determined by treating plants (mean ht, 194.6 cm; mean dia at 3 cm, 13.6 mm) on August 28, 1975. The plants were fully dormant at this time as indicated by the failure of axillary buds to break following defoliation. The treatments (12 plants/treatment) were as follows:

1. Control.

2. Girdle: 1 cm of bark was peeled off the stem 3 cm above the soil surface. Exposed xylem was scraped, covered with petroleum jelly and protected with aluminum foil.

3. Decapitation + IAA: stem was severed 3 cm above the soil surface. The top of the stump was covered with a lanolin paste containing 0.1% Tween 20[2/] a wetting agent, and 1% indole-3-acetic acid (IAA), an auxin. Fresh preparations of IAA and lanolin were reapplied to freshly exposed tissue at 7-day intervals, until October 29.

4. Decapitation + 0: same procedure as in 3 but no IAA.

5. Defoliation - 1: removed all foliage.

6. Defoliation - 2: in addition to removing foliage on August 28, all shoots flushing out the following spring were removed on May 17, 1976.

The plants were kept in the greenhouse until November 6, 1975, when they were moved into pits in the lathhouse for overwintering. At this time a count was made of stem sprouts (from suppressed buds) and of root suckers appearing

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[2/] The use of trade or firm names is for reader information only and does not constitute endorsement by the U.S. Department of Agriculture of any commercial product or service.

above the soil surface. On April 14, 1976, the aspen were removed from the pits and placed on benches in the lathhouse where they remained until the experiment was completed. Counts of stem sprouts and root suckers were repeated on June 10 and July 28. On the last date, the heights of the largest sucker and sprout on each plant were measured.

Results.--Tables 1 and 2 show the effect of treatments on the number of stem sprouts and root suckers produced by aspen on three dates. Very little vegetative regeneration of any kind was evident in November. However, numerous shoot primordia were visible on exposed roots of decapitated, girdled, and defoliated

Table 1.--Experiment 3. *Effect of treatment on number of aspen producing stem sprouts and root suckers after treatment on August 28, 1975. (12 plants per treatment.)*

	Date					
	11/6/75[a]		6/10/76		7/28/76	
Treatment	Stem sprouts	Root suckers	Stem sprouts	Root suckers	Stem sprouts	Root suckers
Control	0	0	0	3	0	2
Defol. - 1	0	2	0	9	0	9
Defol. - 2	0	1	0	11	0	11
Decap. + 0	8	2	11	12	10	12
Decap. + IAA	0	4	1	12	1	12
Gird.	0	7	11	11	6	11

[a] Month/day/year.

Table 2.--Experiment 3. *Effect of treatment on mean number of stem sprouts and root suckers produced by aspen plants treated on August 28, 1975. (12 plants per treatment)*

	Date					
	11/6/75[a]		6/10/76		7/28/76	
Treatment	Stem sprouts	Root suckers	Stem sprouts	Root suckers	Stem sprouts	Root suckers
Control	0	0b[b]	0b	0.2d	0c	0.2d
Defol. - 1	0	0.4ab	0b	3.2c	0c	2.5c
Defol. - 2	0	0.4ab	0b	5.8b	0c	6.2b
Decap. + 0	0.8	0.2b	5.0a	31.0a	3.4a	20.2a
Decap. + IAA	0	0.8ab	0.2b	24.3a	0.2c	21.8a
Gird.	0	1.3a	6.3a	7.5b	1.8b	5.3b

[a] Month/day/year.
[b] Treatments with no common letter are significantly different at 5% level.

plants. A few suckers that developed were less than 1 cm in length and, although they still had green leaves, terminal buds had formed. Stem sprouts on plants in the Decap + 0 treatment, the only treatment to show this type of growth, were elongating when moved outdoors and were killed back by the first frost.

The first evidence of growth activity in the spring was on April 8, when elongating root suckers were observed. This was 10 days prior to the start of bud-break in the tops of the plants. Stem sprouts and root suckers tallied on June 10 showed that decapitated plants produced many more root suckers than any other treatment. Single suckers were initiated on roots of three control plants. Stems sprouts were produced only by girdled (from suppressed buds below the girdle) and decapitated plants.

Application of IAA to decapitated aspen significantly reduced the formation of stem sprouts but did not affect total sucker production. However, IAA did have a significant inhibitory effect on the number of suckers arising from roots near the base of the stumps. The mean number of suckers developing within 1 cm from stumps, were: IAA treatment, 0.9; not treated, 4.3.

Sucker production by plants defoliated in late summer of 1975 was significantly increased by the removal of elongating shoots in the spring of 1976. After shoot removal, new shoots flushed out from suppressed buds on stem and branches of Defol. - 2 plants. There were 22% as many elongating shoots as on control plants.

Mortality generally caused root suckers and stem sprouts to decrease between June 10 and July 28 (Table 2). The decrease was greatest for those plants having the largest number of competing shoots. Contributing to mortality of sprouts on girdled stems was the dying of tops and movement of decay into the base of stems. The tops of 7 out of 12 girdled plants died prior to July 28. The remainder were dead by August 18.

The tallest stem sprouts and root suckers grew on the decapitated plants (Table 3). Suckers developing on roots of Decap. + IAA plants were significantly larger than those on Decap. + 0 plants. Growth of suckers on Decap. + 0 plants was probably reduced by competition from vigorously growing stem sprouts. An extended period of uninhibited growth enabled suckers on Defol. - 2 to be three times larger than those on Defol. - 1 plants. On June 10 terminal buds had formed on most suckers of Defol. - 1 plants, while suckers on Defol. - 2 plants were still elongating.

After the experiment was terminated, roots were examined from a random sample of six plants in each treatment. As was noted in Experiment 1, the root systems of girdled plants had a high percentage of decay. Their roots contrasted sharply with the vigorous appearing roots of plants in the other treatments. Roots of one girdled plant that failed to produce either stem sprouts or root suckers were completely decayed. Suckers were initiated on roots as small as 1 mm. Except for the controls, roots of all treated plants had primordia that failed to develop into shoots.

The tops of girdled plants grew significantly less than the controls in 1976. Terminal growth of control was 24.0 cm, girdled plants, 11.1 cm. Top growth of control and Defol. - 1 plants did not differ significantly.

Table 3.--Experiment 3. *Effect of treatment on growth of stem sprouts and root suckers produced by aspen plants treated on August 28, 1975. Measurements shown are heights (cm) of the tallest shoot on July 28, 1976. (12 plants per treatment.)*

Treatment	Stem sprouts	Root suckers
Control	a/ -	2.1e
Defol. - 1	-	7.7d
Defol. - 2	-	23.8c
Decap. + 0	b/ 52.0a	40.9b
Decap. + IAA	-	64.5a
Gird.	11.3b	19.1c

a/ No sprouts or a negligible number.
b/ Treatments with no common letter are significantly different at 5% level.

SUMMARY AND DISCUSSION

The most important finding from this study is that dormant aspen respond differently than actively growing aspen to sucker-inducing treatments. During active shoot elongation, suckers arose a short time after girdling and decapitation. Removal of foliage and growing shoots during this period did not stimulate suckering. When the plants were treated after bud dormancy, all treatments stimulated sucker initiation on roots, as indicated by the presence of shoot primordia, but shoot elongation was suppressed until the following spring. The suppression of shoot development supports the author's hypothesis that growth and extension of a primordium is more sensitive to inhibition than is initiation of the primordium (Schier 1975). Regulation of dormancy may be controlled by a balance between endogenous inhibitors, such as abscisic acid, and growth-promoting substances, especially gibberellins (Giertych 1974). Suckering in aspen is inhibited by abscisic acid (Schier 1973d). Gibberellins appear necessary for sucker growth and can reduce inhibition caused by abscisic acid (Schier 1973a, 1973d). Dormancy is broken by low winter temperatures, which lower the inhibitor: growth-promoter ratio.

An apparent exception to the above observations was the formation of suckers on aspen root cuttings (10 X 1 to 2 cm) collected in late summer or fall (Schier and Zasada 1973). Sucker development was not suppressed and equalled or exceeded the numbers produced in June or July. Possibly inhibitors of suckering became inactivated after the cuttings were excised. Hormone metabolism may be entirely different in large-diameter root segments from mature trees than it is in the intact root system of small trees.

In addition to the conflicting results cited above, the results of this study must be reconciled with Eliasson's (1971b) findings that the induction of dormancy in European aspen (P. tremula L.) induces root suckering. Young plants (first-year rooted cuttings) growing in culture solutions became dormant when exposed to short days. Several weeks after buds had set, suckers emerged from the roots. Suckers apparently were produced because dormant shoots produce little auxin. Hormonal changes in the plants that caused terminal and lateral bud dormancy did not affect the suckering capacity of roots, as it apparently had in the current study. According to Eliasson's results, the dormant control plants in this study should have produced suckers. The reason the plants in the two studies responded differently to short days may have been because of differences in the species, age of the plants, or cultural methods used in the experiments. Any of these factors could have affected the results of the respective studies by their effect on hormone balances or the responsiveness of tissue to sucker-inducing stimuli.

Even such drastic treatments as multiple defoliation did not stimulate suckering when plants were defoliated early in the summer. After bud set, however, a single defoliation induced sucker initiation, although shoot elongation was delayed until spring. Apparently auxin concentrations in roots of young trees are maintained at inhibitory levels if lateral buds flush immediately after treatment. Apical control appears to be weaker in older and larger trees, because insect defoliations are known to stimulate suckering in mature trees even when followed by a second set of foliage. The distance that auxin must be transported (crown to roots) in mature trees, in comparison to young trees, probably means that in mature trees any injury that interrupts the auxin supply is more likely to reduce auxin below inhibitory level in roots.

Late summer defoliation probably resulted in sucker initiation because the major source of auxin in these plants, the leaves, was eliminated. The suckers elongated during warm weather of the following spring, prior to bud break and reestablishment of apical control by the crown. The period before the buds flush out, when auxin concentrations are at a low level in the roots and temperatures are high enough for sucker development, may be the time suckers were produced by the control plants. It also may be an important period for sucker initiation in relatively undisturbed clones under natural conditions, especially if there is a sudden spring thaw. Removal of elongating shoots from previously defoliated plants probably kept auxin concentrations in the roots at low levels and, therefore, significantly increased the number and height growth of suckers.

Regardless of the time of treatment, decapitated plants produced far more suckers than girdled ones. Similar results have been reported by others. Farmer (1962) achieved less success in stimulating suckering by girdling roots than by cutting them. Smith et al. (1972) reported that plots where mature trees were girdled produced only 25% as many suckers as those that were clearcut. Farmers in the Mid-West have used girdling to eliminate unwanted poplar trees because girdled trees produced far fewer root suckers than those that were cut.

It is doubtful that little, if any, auxin moved past the girdle via the xylem or pith (Eliasson 1971b, Sheldrake 1973). Consequently there must be other explanations to account for fewer suckers developing on roots of girdled plants than on decapitated ones. Substances important to sucker initiation and

growth, such as nitrogenous compounds and cytokinins, which are synthesized in roots, very likely continued to move upward in the transpiration stream in girdled plants. Whereas, in decapitated plants, these substances accumulated in the stumps and roots (Eliasson 1971b, Farmer 1962). Therefore, roots of the decapitated plants were in a better condition to produce suckers. Stumps of the decapitated plants probably accumulated cytokinins; therefore, were the only treated dormant plants to produce stem sprouts. High levels of cytokinins counter the effect of inhibitors in dormant tissue (Khan 1971).

Poor development of suckers on roots of girdled plants caused large portions of their root systems to die because photosynthates were insufficient to maintain essential metabolic processes. The tops that lived during most of the summer probably contributed to root mortality by continuing to drain the roots of food reserves and other growth substances. Root losses, particularly loss of fine roots that are important sources of water, growth regulators, and nutrients, suppressed sucker formation and growth and resulted in eventual death of the tops. In a decaying parent root system, the ability of suckers to establish independent root systems (by stimulating the formation of adventitious roots on stems and new laterals on parent roots) may enable them to survive (Sandberg 1951, Schier and Campbell 1978).

Very little success was achieved in suppressing suckering of decapitated plants by the application of IAA. To have further reduced production probably would have required treating the stumps with IAA for the duration of the study (Farmer 1962). Nevertheless, short-term treatment almost completely suppressed stump sprouting and significantly reduced root suckering around the base of the stumps. The results indicated that, as the distance from point of application increased, the effectiveness of exogenous IAA rapidly decreased. It was surprising that fall applications of IAA were so effective in inhibiting stump sprouting, considering reports that exogenous IAA is rapidly inactivated (Davies 1972, Eliasson 1972, Morris et al. 1969). Perhaps the concentration of IAA was toxic and bud development was irreversibly inhibited.

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